Chapter 4
Circatidal and Circadian Rhythms in Crustacean Swimming Behavior

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Abstract Marine animals occasionally exhibit complicated temporal activity patterns, which are affected by both tidal and solar day cycles. The cumacean *Dimorphostylis asiatica* (Crustacea, Peracarida) swims up in the water column around nocturnal high tides. In the laboratory, the animals show a circatidal swimming rhythm, entrained by hydrostatic pressure stimulus. During recording, the daily bimodal circatidal rhythmicity spontaneously changes to a circadian daily unimodal light-entrained rhythm.

Keywords Circadian • Circatidal • Entrainment • Splitting • Swimming activity rhythm

4.1 Introduction

Outputs of endogenous biological rhythms entrained by environmental tidal cycles, that is, circatidal rhythms, have been reported in many marine and semiterrestrial organisms (Neumann 1981; Morgan 1991; Palmer 1995; Naylor 2010). Occasionally, circatidal rhythms exhibit a rather complicated temporal pattern corresponding to environmental tidal and solar day periodicities.

The swimming activity rhythm of two sand beach peracarid crustaceans, the amphipod *Synchelidium* sp. and the isopod *Excirolana chiltoni*, has a bimodal activity pattern, and the two activities are conjugated (i.e., free-run together). The amplitudes of the conjugated activities are unequal; that is, one of two activity bouts on a single day is more intensive or longer lasting than the other. The rhythm occasionally changes between daily bimodal and daily unimodal patterns spontaneously, which was explained as environmental adaptation of the rhythmicity to the mixed semidiurnal tide that gradually changes according to the lunar phase (Enright 1962, 1972, 1976; Klapow 1972). Similar daily bimodal circatidal rhythms with unequal amplitudes have been reported in a few marine animals (Holmström and Morgan 1983a; Palmer and Williams 1986a; Northcott 1991; Sato et al. 2008).

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Marine animals are exposed to solar day cycles as well as to tidal cycles. As a result, their activity rhythms occasionally exhibit complicated temporal patterns including tidally synchronized and solar day-synchronized rhythmic components, other than the only tide-synchronized complicated rhythmic patterns already mentioned (Barnwell 1966; Stillman and Barnwell 2004; Zann 1973; Barlow et al. 1986). In the terrestrial crab *Sesarma*, timing of larval release, synchronized with the night high tide, is entrained by solar day cycles as well as moonlight cycles (Saigusa 1986, 1988). In the shore crab *Carcinus* and some fishes kept under nontidal conditions, their daily bimodal circatidal locomotor rhythm changes to daily unimodal circadian rhythm (Naylor 1958; Gibson 1971, 1973). In the daily bimodal circatidal locomotor rhythm of the mangrove cricket *Apteronemobius asahinai*, the uneven amplitude of the conjugated activity is thought to be generated by a circadian component of the underlying pacemaker (Takekata et al. 2012).

Studies of the complicated rhythmicity as just mentioned, may provide some new insights into the evolutionary trait of circatidal clocks as well as their current divergence. In this chapter, I describe the spontaneous change of swimming activity rhythm between circatidal and circadian in the cumacean *Dimorphostylis asiatica* (Crustacea, Peracarida) from the Seto Inland Sea of Japan.

4.2 Temporal Emergence Pattern in the Field and Its Seasonal Variation

Planktonic animals show diurnal vertical migration, based on swimming upward in the water column (Pearcy 1970; Enright 1977). Tidal planktonic animals may perform similar movements. Cumaceans, consisting of about 1,500 species, live in the surface of sandy or muddy sea bottoms, from the intertidal to the hadal zone. The genus *Dimorphostylis*, consisting of 29 species, lives in shallow water in the Western Pacific and Indian Ocean, currently with only one deep-sea species (Băcescu 1988; Gamô 1968; Akiyama 2011). Field studies on shore and shallow-water cumacean species have also shown diurnal vertical migration, based on their nocturnal upward swimming (Corey 1970; Yoda and Aoki 2002). The temporal emergence pattern of *D. asiatica* from the Seto Inland Sea, at 1–3 m depth, where a mixed semidiurnal tide about 1.5–3.5 m in amplitude recurs, was investigated using an electric torch lamp attracting male specimens (Akiyama and Yoshida 1990). The emergence pattern in the field shows rather complicated rhythmicity, which varies with seasons (Fig. 4.1). In winter and spring, the animals emerge around the time of the night high tide every day, showing a daily unimodal tidal rhythm with a period of about 24.8 h (Fig. 4.1a). A similar emergence pattern in shallow-water habitats has been reported in other tiny crustaceans such as a cladoceran, a copepod, an amphipod, and a few crab larvae (Saigusa and Oishi 2000; Saigusa 2001).

In contrast to the emergence pattern in winter, which shows close synchrony with night high tides, in autumn the emergence mainly occurred within 1 h just after sunset (Fig. 4.1b), showing solar day synchronized rhythmicity. Small portions of the
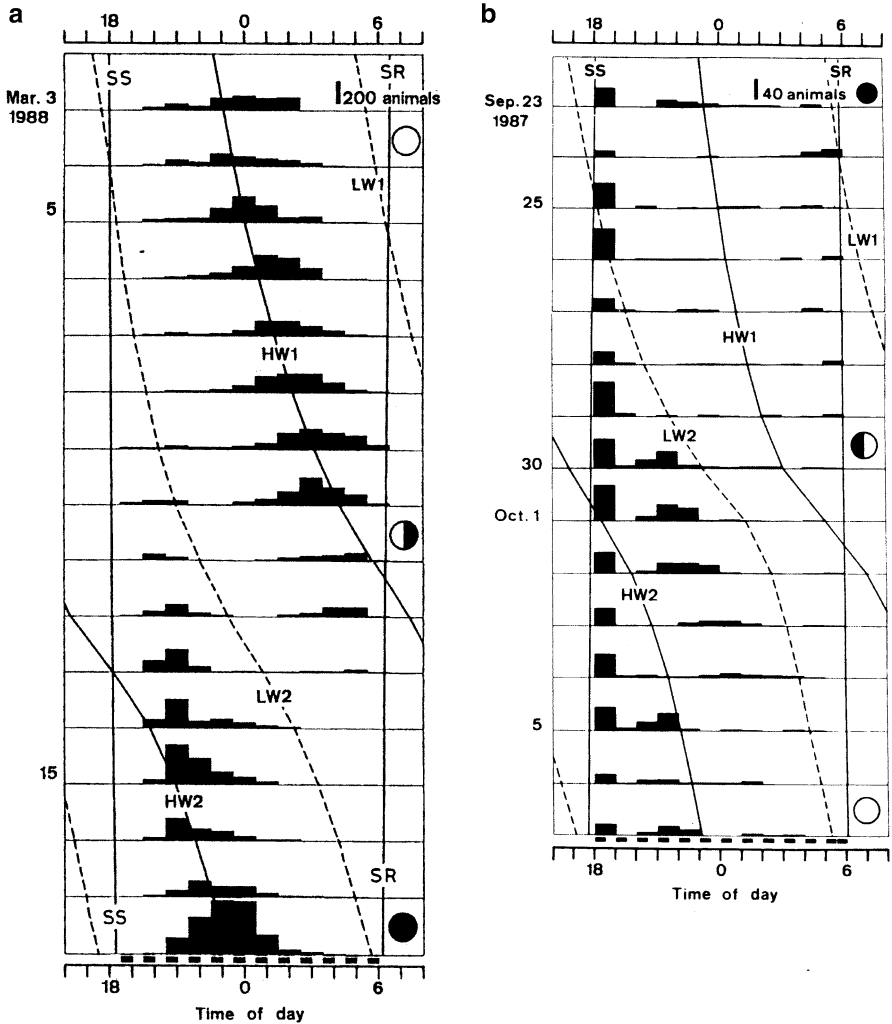
Fig. 4.1 Temporal emergence pattern of *Dimorphostylis asiatica*. Emergence during each time interval was indicated as number of adult male animals collected with an electric torch lamp for 30 min. (**a**) Emergence pattern in winter. *HW* high water, *LW* low water, *SS* sunset, *SR* sunrise; *open circle* full moon, *closed circle* new moon (Akiyama 1995). (**b**) Emergence pattern in autumn. (From Akiyama and Yoshida 1990; reproduced by courtesy of The Marine Biological Laboratory, Woods Hole, Massachusetts)

animals emerge during ebb (between 30 September and 4 October in Fig. 4.1b) or flow tides (5–7 October in Fig. 4.1b). Seasonal variation of tide-synchronized emergence rhythm between day and night in the field was also reported in the emergence rhythm of the marine midge *Clunio tsushimensis* (Oka and Hashimoto 1959; Saigusa and Akiyama 1995). In this case, the seasonal change of the temporal emergence

pattern was related to the seasonal change of temporal tidal pattern. The height of the daytime low tide is lower than the height of the night low tide in late spring and summer, whereas in winter the opposite tidal pattern occurs at the sampling site.

4.3   Free-Running Activity Rhythm and Temperature Compensation

Diurnal vertical migration of many marine organisms based on their swimming activity shows circadian rhythmicity in the laboratory (Enright and Hamner 1967). Male specimens of *D. asiatica* show a clear swimming activity rhythm in constant darkness, indicating that this behavior is also governed by endogenous clocks (Fig. 4.2). In this species, the rhythmicity is regarded as circatidal but not circadian, which is based on the observations that in the presence of tidal periodicity (1) the daily bimodal activity pattern has a period length close to the environmental tidal period (12.4 h) and (2) the onset of activities coincides with the expected high tide on the first day of the recording.

The calculated free-running period of the daily bimodal rhythm was approximately 11.5 h on average, 1 h shorter than the environmental tidal cycle (Fig. 4.2a). Coincidence of the endogenous swimming activity with the expected high tide was rapidly lost during the first 1 or 2 days of the recording. Previous studies on the circatidal rhythms have focused on close similarity of the free-running periods to environmental tidal periods (Palmer 1995; Naylor 2010). As an extreme case, the sandy beach isopod *Excirolana* shows a temporal free-running activity pattern that is very similar to the complicated environmental tidal pattern (Enright 1972). The rather short free-running period of *D. asiatica* in its daily bimodal rhythm shown in my study may be a generic characteristic. An estuarine *Dimorphostylis* sp. from the Seto Inland Sea of Japan, kept in seawater at 15‰ salinity in the laboratory, exhibited a daily bimodal free-running rhythm with a period shorter than 24 h, which was similar to that of *D. asiatica* (T. Akiyama, unpublished data).

The specimens collected in all seasons exhibit distinct daily bimodal activity rhythms, at least during the early days of recording, and onsets of the first batch of activity on the first day of recording occur about 0.5 h before the expected high tide throughout a year (Akiyama 2004), which suggests that the circatidal clock of the animals operates in the field in all seasons. Therefore, the seasonal variation of emergence pattern in the field (shown in Fig. 4.1) should be caused by the environmental factors that directly affect their swimming behavior, not via endogenous clocks of the animals. In another peracarid crustacean, *Corophium voltator*, seasonal variation of circatidal activity rhythm was also observed in the laboratory (Holmström and Morgan 1983a).

Although the environmental tide in the Pacific Coast of southern Japan is a mixed semidiurnal tide, the bimodal circatidal swimming rhythm of most specimens is characterized by equal amplitude of two conjugated activities (Fig. 4.2a). A small portion of the specimens exhibit daily bimodal rhythms with unequal amplitude of conjugated activities. However, this phenomenon would not necessarily

Fig. 4.2 Free-running swimming activity rhythm of two specimens of *Dimorphostylis asiatica* under constant darkness (Akiyama 1995). (**a**) A specimen that retained daily bimodal activity pattern throughout 20 days of recording. (**b**) A specimen whose activity pattern changed from daily bimodal to unimodal on days 10–12. *Arrowheads* indicate times of high water at the sampling site
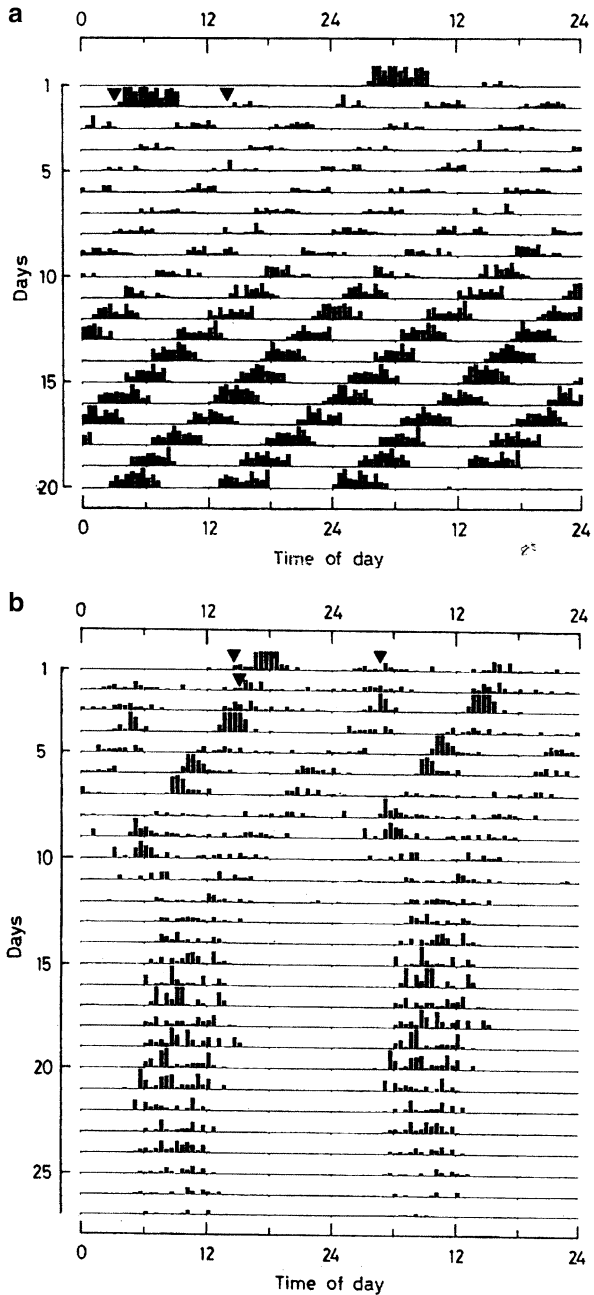
be related to the environmental tidal pattern. In the mangrove cricket, a daily bimodal rhythm with unequal amplitude is explained as modification of the circatidal rhythm by a circadian pacemaker (Takekata et al. 2012).

In *D. asiatica*, the daily bimodal activity rhythm in about 90 % of the specimens examined spontaneously changed to the daily unimodal rhythm, within 10 days (it took 11–12 days in the specimen shown in Fig. 4.2b). In contrast to that just described for *Excirolana*, the change of the rhythmic pattern does not seem to be related to the environmental tidal pattern because the bimodal rhythms with equal amplitude of conjugated activity occur in most specimens in spite of the mixed semidiurnal tide at the collection site.

As in circadian rhythms, the free-running period of circatidal rhythms shows relatively small change according to change of ambient temperature (Naylor 2010). The free-running period of the daily bimodal rhythms in *D. asiatica* is 23.1 ± 1.6 and 22.9 ± 1.1 h at 10 and 15 °C, respectively. In the daily unimodal rhythm, the period is 25.5 ± 1.8 and 23.8 ± 0.6 h at 10 and 15 °C, respectively (Akiyama 1995). Temperature compensation was shown in the free-running periods of the daily bimodal and unimodal rhythms; Q_{10} values were 1.02 and 1.15, respectively, even though the latter value is slightly larger than values for circadian and circatidal rhythms of other animals. The difference in the compensation between the daily bimodal and unimodal free-running rhythms suggests that these rhythms are governed by pacemakers with different molecular oscillation systems. Otherwise, if identical pacemaker(s) govern the different forms of rhythmicity, neural components other than the molecular oscillation system may generate different periodicity. Unfortunately, previous studies on circadian and circatidal rhythms have not focused on comparison of temperature compensation accompanied by change of rhythmicity between daily unimodal and daily bimodal in a single species.

4.4 Administration of Hydrostatic Pressure Stimulus

Although circadian rhythms are dominantly entrained by sunlight (Binkley 1990), circatidal rhythms are phased by various kinds of time cues, such as mechanical agitation caused by water flow and wave action (Enright 1965, 1976; Klapow 1972; Hastings 1981; Morgan and Cordiner 1994), change of ambient temperature (Holmström and Morgan 1983b, c; Bolt et al. 1989), salinity change (Taylor and Naylor 1977; Bolt and Naylor 1985; Bolt et al. 1989), and periodic inundation of intertidal habitat (Holmström and Morgan 1983c; Yoshioka 1989; Chabot et al. 2008; Sato et al. 2009). Tide-synchronized larval release of a few species of terrestrial and semiterrestrial crabs is additionally phased by moonlight cycles or solar day sunlight cycles (Saigusa 1986, 1988, 1992).

For marine animals living in shallow, calm habitats, including *D. asiatica* from the Seto Inland Sea of Japan, periodic change of hydrostatic pressure stimulus caused by gradual fluctuation of tidal height would be a reliable tidal time cue for their circatidal clocks. The swimming behavior of tiny crustaceans responds to sudden change of hydrostatic pressure (Enright 1961; Digby 1972; Morgan 1984). Successful entrainment by a 12.5-h cycle of sinusoidal change of hydrostatic pressure was reported for the swimming behavior of an estuarine amphipod, *Corophium*

(Morgan 1965). Thereafter, entraining effects by hydrostatic pressure cycles on circatidal rhythms have been reported in the shore crab *Cacinus* (Naylor and Atkinson 1972), the horseshoe crab *Limulus* (Chabot and Watson 2010), and a few fish species (Gibson 1971, 1984; Northcott 1991; Northcott et al. 1991a, b).

A 12.5-h cycle of sinusoidal change of hydrostatic pressure of 0.3 atm, equivalent to 3-m amplitude of tidal height, entrains the circatidal swimming rhythm of *D. asiatica* (Akiyama 2004). Most specimens (*N*=41) examined displayed daily bimodal activity with periods of 24.9±0.6 h, as shown on days 1–10 in Fig. 4.3a, b,
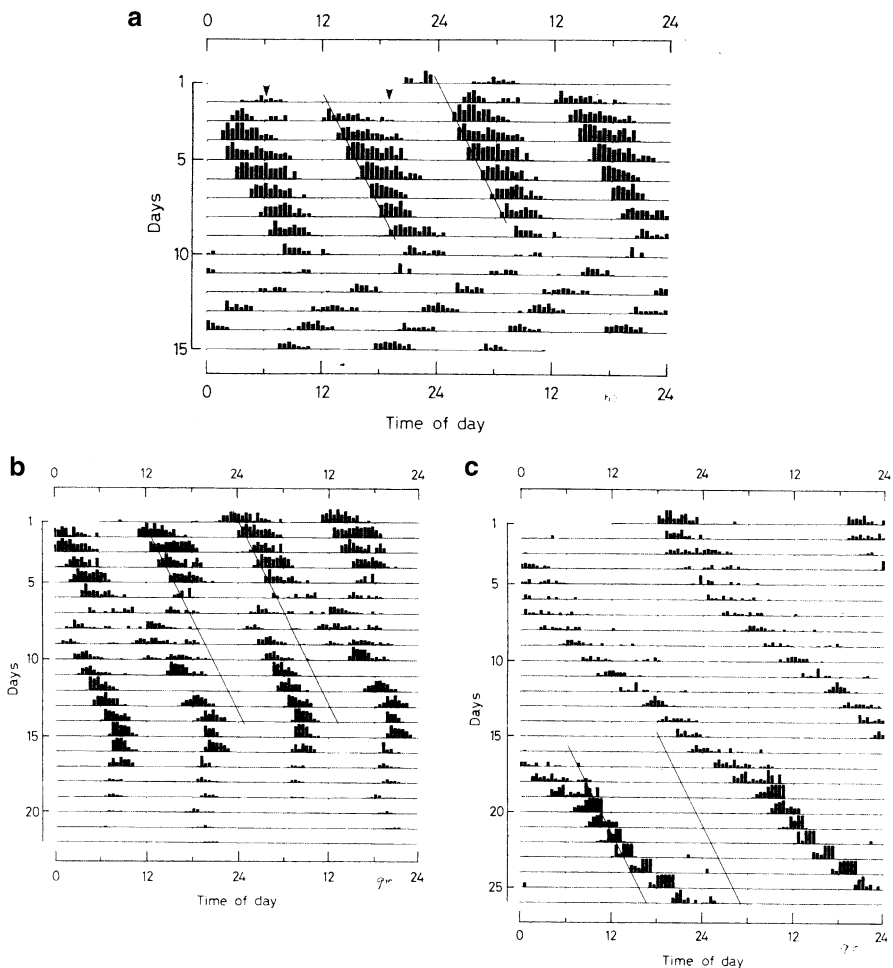
Fig. 4.3 Three *Dimorphostylis asiatica* specimens exposed to a 12.5-h cycle of sinusoidal change of hydrostatic pressure with 0.3-atm amplitude, under constant darkness. *Oblique lines* indicate times of maximum hydrostatic pressure (Akiyama 2004). (**a**, **b**) Specimens exhibiting daily bimodal rhythmicity. (**c**) Specimen exhibiting daily unimodal rhythmicity

which is about 2 h longer than the free-running period of the daily bimodal rhythm. The activity onsets of the animals occur shortly before the time of the maximum hydrostatic pressure. Correspondingly, the onset of the first bout of activity in the free-running rhythm occurs 0.5 ± 2.1 h before the expected high tide in all seasons (Akiyama 2004). Thus, a hydrostatic pressure cycle can clearly entrain the circatidal rhythm of this species. It therefore appears that the entrained bimodal activity pattern is characterized by simple 12.5-h rhythmicity, with roughly equal amplitude and duration of the two conjugated activity bouts.

A small portion of individuals exhibit a daily unimodal activity rhythm while they are exposed to the hydrostatic pressure cycles (Fig. 4.3c). The activity period is 25.9 ± 1.6 h ($N = 11$), which is close to the free-running period at 10 °C, suggesting that the pacemaker that governs the unimodal activity pattern is not phased by hydrostatic pressure stimulus.

Phase responsiveness of circatidal rhythms to single pulses of zeitgebers has been examined and summarized as phase-response curves (PRCs) in an isopod *Excirolana* (Enright 1976), an estuarine amphipod *Corophium* (Holmström and Morgan 1983b), the rocky shore crab (Naylor and Williams 1984), a shore fish (Northcott et al. 1991b), the mangrove cricket (Sato et al. 2009), and a few additional marine species. The results seem to be rather simple; that is, PRCs of circatidal rhythms are similar to those of circadian rhythms, but on a 12.4-h time base.

In *D. asiatica*, phase responsiveness of the swimming rhythm to a 4-h hydrostatic pressure pulse (sudden increase and decrease of hydrostatic pressure of 0.3-atm amplitude) was examined. A unique characteristic of the phase responsiveness was that two conjugated activity bouts occasionally respond to the 4-h pulse of the hydrostatic pressure stimulus differently. The specimen shown in Fig. 4.4a shows a different magnitude of phase delay, and another specimen (Fig. 4.4b) shows phase advance and phase delay for each conjugated activity bout, respectively. These data suggest that the approximately 12-h rhythm, in appearance, of *D. asiatica* is composed of two 24-h pacemaker components (Fig. 4.4b).

PRCs of *D. asiatica* specimens (indicated on a 24-h time base; the onsets of daytime activity on the first day of recording are determined as circadian time 12), in which daily bimodal rhythm persisted after administration of a hydrostatic pressure stimulus have an obscure form (Fig. 4.4e). Both phase advance and delay occur around circatidal times 8 and 20, in contrast with the entraining ability of 12.5-h cycles of 'sinusoidal' change of hydrostatic pressure on the daily bimodal rhythm within 1–2 days of treatment (Fig. 4.3a). Apparently, the animals perceive a gradual increase or decrease of hydrostatic pressure as the dominant tidal time cue. Thus, the obscure PRC pattern may be a consequence of the sudden increase or decrease of hydrostatic pressure in this experiment.

Another possible factor causing the obscure form of the PRC is the unstable phase relationship between the entrained activity and the hydrostatic pressure pressure cycle: some specimens entrain the swimming activity to the phase of increasing pressure, whereas other specimens entrain to the phase of decreasing pressure, and rarely were both phase relationships observed sequentially in a single specimen (Fig. 4.3b). Such a flexible phase relationship between entrained rhythmicity and environmental cycles is also possibly attributed to the weak phase-setting effect of
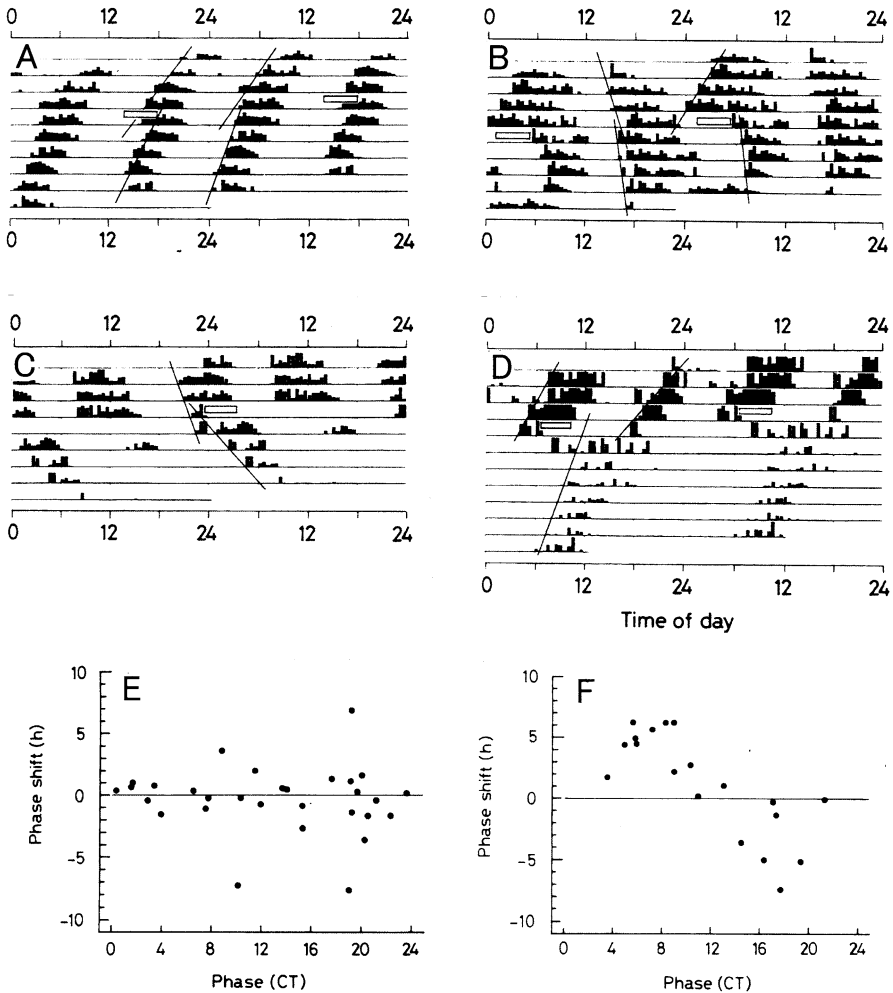
Fig. 4.4 Phase-setting effect of a 4-h pulse of hydrostatic pressure with 0.3-atm amplitude on the swimming activity rhythm of *Dimorphostylis asiatica* (Akiyama 1997). (**a–d**) Activity pattern of four specimens. *Rectangles* indicate times of treatment. *Oblique lines* are linear regression lines on the successive onsets of swimming activities. (**e, f**) Phase–response curves (*PRCs*) of the daily bimodal rhythms to the hydrostatic pressure pulses. CT circadian time. Time of activity onsets near the time of treatments was determined as CT12. (**e**) PRC of specimens that retained a daily bimodal rhythm after treatment (**a, b**). (**f**) PRC of specimens that exhibited a daily unimodal rhythm after treatment (**c, d**)

the hydrostatic pressure stimulus, as reported in the diurnal–nocturnal conversion of the circadian rhythm of fishes (Sánchez-Vázquez et al. 1995; Iigo and Tabata 1996).

In nearly half the treated specimens, daily bimodal activity rhythms changed to daily unimodal patterns immediately after administration of hydrostatic pressure pulses (Fig. 4.4c, d). For these specimens, phase advance and delay occur around circadian times 8 and 18 (Fig. 4.4f), respectively, showing that the PRC form is on

a 24-h time base (Fig. 4.4f). A similar change of activity between daily unimodal and bimodal patterns, associated with treatment with a single pulse of tidal time cue, was also observed in *Excirolana*. However, in *Excirolana* the PRC pattern was simply 12.4-h intervals (Enright 1976). The PRC form of *D. asiatica* may be the first case of a PRC pattern of circatidal rhythm on a 24-h time base, suggesting that the animals recognize daytime or nighttime high water, even when the animals are exhibiting only circatidal rhythms. In view of adaptive significance, the PRC of the 24-h time base suggests that the animals recognize 'daytime' high tides as the more reliable time cue. During nighttime, swimming in the water and settling on the sea bottom at different depths would result in sudden change of environmental hydrostatic pressure, which would disturb the sensing of tidal time cue(s).

In conclusion, in contrast to the daily bimodal activity rhythm, the daily unimodal rhythm is not entrained by a single pulse of a 4-h hydrostatic pressure stimulus, which agrees with the fact that the unimodal rhythms are not entrained by 12.5-h hydrostatic pressure cycles (Akiyama 1997).

4.5   Administration of Light Stimulus

Current knowledge on phase-setting effects of light stimuli on circatidal pacemakers is limited, except for a few species. In the horseshoe crab *Limulus*, light–dark cycles entrained the daily bimodal circadian rhythm in a small portion of specimens (Chabot et al. 2007; Chabot and Watson 2010). Shift of light cycles causes phase shift of the larval release rhythm in the terrestrial crab *Sesarma* (Saigusa 1986, 1988), and this phenomenon is possibly related to their nontidal habitat, where the phase relationship of moonlight and solar day cycles can be a useful time cues.

Many *D. asiatica* specimens kept under light–dark (LD) cycles of LD 12:12 (about 1,000 lx for light phase; complete darkness for dark phase) exhibit daily unimodal activities during the dark phase, even during the first few days of recordings (Akiyama 2004). In contrast, the temporal activity pattern of the specimens kept under light cycles with a shorter photoperiod, such as LD 6:18, shows that the daily bimodal activity free-runs with periodicities shorter than 24 h. In the specimen shown in Fig. 4.5a, the activity rhythm free-ran on days 1–10, and entrained to the hydrostatic pressure cycle thereafter, with inhibition of activities during light phase throughout the recording. Thus, the unimodal activity pattern under LD 12:12 is the result of a masking effect that is caused by direct inhibition of activity by light. Specimens exposed to the 12.5-h hydrostatic pressure cycles and light cycles with longer photoperiod, such as LD 12:12, exhibit a temporal activity pattern similar to the tide-synchronized emergence pattern in the field, suggesting that the animals use these two cycles as important time cues in the field. Small bursts of activity shortly after lights off (on days 7–15 in Fig. 4.5b, also seen in Fig. 4.5a) also agree with the emergence just after sunset in the field (Fig. 4.1b).

The masking effect by light has been well documented in circadian rhythms (Page 1989). Nocturnal activity by direct suppression of the swimming activity by
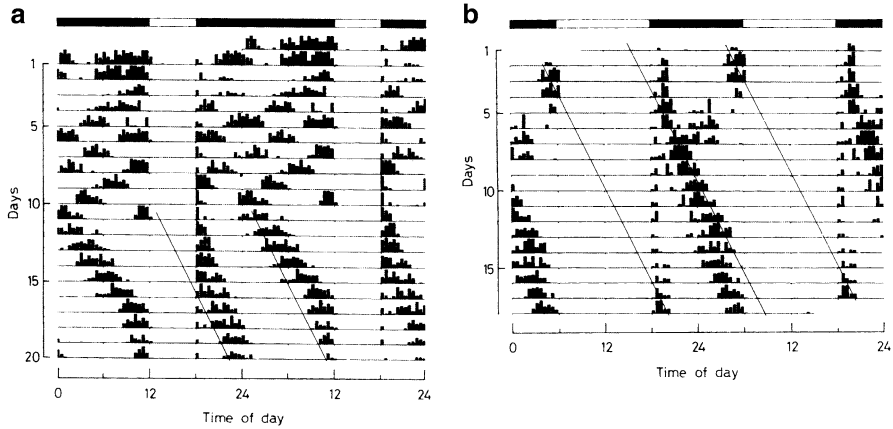
Fig. 4.5 Activity records of *Dimorphostylis asiatica* exposed to different light cycles and the 12.5-h hydrostatic pressure cycle. (**a**) A specimen kept under light regime LD 6:18; on day 10, the hydrostatic Zeitgeber was added. (**b**) A specimen kept under LD 12:12. *Oblique lines* indicate the times of maximum hydrostatic pressure (Akiyama 2004)

light stimuli during daytime is also observed in the diurnal vertical migration in shallow-water planktonic animals (Enright and Hamner 1967).

A problem in studies on circatidal rhythms is their noisy, short-life nature (Neumann 1981). Such noisiness may not reflect the output of an inferior clock mechanism but rather internal desynchronization of clock components in single specimens. In the eel pout *Zoarces viviparus*, desynchronized, arrhythmic swimming activity spontaneously changes to rhythmic daily unimodal or bimodal activity (Cummings and Morgan 2001). Tide-synchronized endogenous pacemakers in some species may have evolved by reorganizing such independent, desynchronized clock components.

For the daily bimodal rhythm in *D. asiatica*, no phase-setting effect of a single 4-h light pulse was observed (Akiyama 1997). Administration of the light pulses did not cause a change of the activity pattern into daily unimodal, which was occasionally observed by administration of the hydrostatic pressure pulses.

In contrast to the daily bimodal rhythm, a single 4-h light pulse administered to the specimens exhibiting a daily unimodal activity rhythm produces distinct phase advances (Fig. 4.6a) and delays (Fig. 4.6a, b). The PRC pattern (Fig. 4.6c) indicates that the 4-h light pulse completely reset the rhythm so that the onset of the activities occurred just after lights-off of each pulse. Considering no phase-resetting ability of hydrostatic pressure stimuli, the *D. asiatica* daily unimodal rhythm is definitely a circadian, light-phased rhythm. Occurrence of the unimodal circadian rhythms under nontidal conditions is similar to that in the shore crab *Carcinus* (Naylor 1958). However, the underlying pacemaker structure of these species would be rather different (see Sect. 4.6).

When the specimens were exposed to the hydrostatic pressure cycle under light–dark cycles (LD 6:18, 12:12), an increased number of specimens were active during
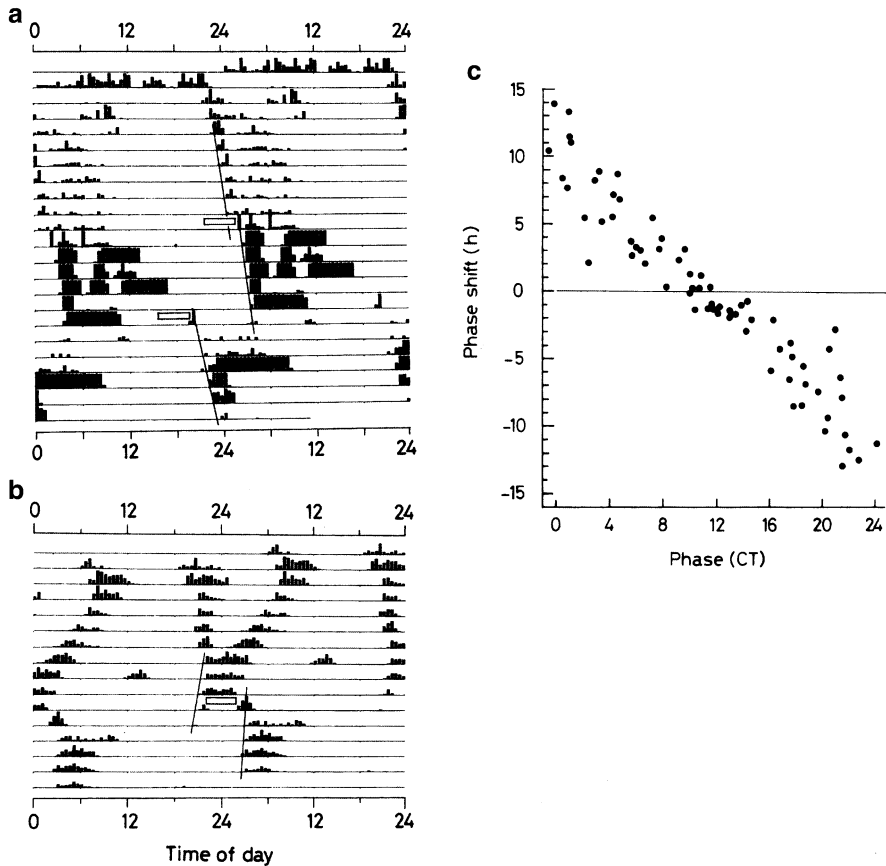
Fig. 4.6 Phase-setting effect of a 4-h light pulse on the daily unimodal swimming rhythm of *Dimorphostylis asiatica* kept in constant darkness. (**a**, **b**) Activity records of two specimens. *Rectangles* indicate time of treatment. *Oblique lines* are linear regression lines on the successive onsets of swimming activities. (**c**) Phase-response curve of the daily unimodal swimming rhythm to 4-h light pulses (Akiyama 1997)

the pressure-increasing phase compared to the number of specimens kept under constant darkness (Akiyama 2004). This observation suggests that light also affects the *D. asiatica* circatidal rhythm, in addition to responsiveness to hydrostatic pressure pulses, as indicated by the 24-h time base of the PRC (Fig. 4.4f).

4.6 Tidally Synchronized Circadian Rhythm?

The periodicity of circatidal clocks is closely related to that of circadian, solar day clocks. In addition, circadian clocks are occasionally phased by time cues other than light–dark cycles. Enright (1976) proposed that the locomotor activity rhythm of

Excirolana is "a tidally-synchronized circadian rhythm," because the "locomotor activities repeat with circadian intervals." Thereafter, few studies have focused on this hypothesis.

The 'splitting' phenomenon, that is, a gradual change of circadian temporal activity between daily unimodal and bimodal rhythms, has been reported for circadian rhythms of some terrestrial animals (Pittendrigh and Daan 1976; Underwood 1977). In these cases, the split and fused rhythms are governed by identical pacemaker(s) with a different phase relationship. In circatidal rhythms, a few genera of intertidal crabs, *Helice*, *Macrophthalmuas*, and *Uca*, and the horseshoe crab *Limulus*, showed two (or more) conjugated activities. Their free-running periods were slightly different from each other, and occasionally fused or split (Palmer and Williams 1986a, b, 1988; Chabot and Watson 2010). Interpreting the splitting in locomotor rhythms, Palmer and Williams (1988) explained that these rhythms were governed by two (or more) coupled pacemaker(s) with about a 24.8-h period, rather than a 12.4-h period, and the periodicity was called 'circalunidian.' Although the approximately 24-h period of the 'circalunidian' clocks is the same as the period of circadian clocks, evolutionary relationships of these clocks have not been investigated or discussed sufficiently.

Naylor and colleagues demonstrated that independent circatidal and circadian clocks govern locomotor rhythms in the shore crab *Carcinus* (Reid and Naylor 1989; Naylor 2010). The essential period of the tidal pacemaker was supposed to be simply 12.4 h. The rigid 12.4-h periodicity may be partly related to the regular semidiurnal tide of their habitat in the eastern North Atlantic (Barnwell 1976). Further comparative studies of circatidal rhythms with various environmental tidal patterns, including animals distributed in the geographic regions characterized by diurnal tide, would be helpful to reveal the rigidness of rhythmicity and the underlying mechanisms of circatidal rhythms.

In the swimming activity of *D. asiatica*, circatidal and circadian rhythms do not occur simultaneously. In addition, the daily bimodal, circatidal rhythm composed of two pacemaker components of about 24 h occasionally fuse to become one daily unimodal circadian rhythm for a few or several days (Fig. 4.6b). Rarely, the unimodal rhythms further split again to become a daily bimodal rhythm (Akiyama 2004). It is plausible that those two rhythms are governed by identical pacemaker(s), as well as in the cases of splitting in rodents and crabs, suggesting that *D. asiatica* has developed a 'tidally synchronized circadian clock' or 'solar day-synchronized circatidal clock.'

Diurnal vertical migration of marine organisms dominantly exhibits solar day-synchronized rhythmicity rather than tide-synchronized rhythmicity. In cumaceans, habitats of most species are rather deep, exceeding 100 m in depth (Băcescu 1988, 1992). However, certain genera such as *Dimorphostylis* might have been adapted to their life to shallow, tide-affected area. Thus, considering cumacean habitats, the biological clock of *D. asiatica* seems to be a 'tidally synchronized circadian clock.'

Recently, molecular analysis, using RNAi of the *per* gene, on the locomotor activity rhythm of the mangrove cricket composed of both circatidal and circadian components, revealed that the molecular oscillation system of the cricket's 12.5-h recurring circatidal clock does not include *per* products, showing that it is different from the

general insect circadian clock (Takekata et al. 2012). This finding and succeeding results on the circatidal rhythm of mangrove crickets (Takekata et al. 2014) suggest that at least some marine organisms may have developed a 12.5-h period clock system, composed of molecular parts that are different from circadian clocks. However, considering various temporal patterns of environmental tidal cycles, and circatidal rhythms synchronized with those complicated time cues, further studies should be necessary to elucidate the evolution of traits and the divergence of circatidal clocks.

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